

Morphological Divergence and Predator-Induced Shell Repair in *Alia carinata* (Gastropoda: Prosobranchia)

by

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Abstract. Morphological divergence of shell carina between protected harbor and exposed rocky cove populations of *Alia carinata* (Hinds, 1844) at Bodega Bay was documented by assigning and comparing keel ratings. The harbor population had a significantly higher frequency of highly keeled individuals than the cove population. Shell-scar frequency data provide evidence that predation intensity is greater in the harbor, and we suggest a relationship between morphological divergence and differential predation pressure.

INTRODUCTION

POLYMORPHISM HAS BEEN observed in geographically separated populations of many gastropod species (*e.g.*, KITCHING *et al.*, 1966; SPIGHT, 1973; KITCHING & LOCKWOOD, 1974; HELLER, 1976; VAN MARION, 1981; REIMCHEN, 1982). Specific morphs often seem to be particularly well adapted to their local environment (*e.g.*, KITCHING & LOCKWOOD, 1974). Compelling evidence for this assertion comes from studies of the defensive morphology of gastropods from sites with and without abundant predators. Where predators such as durophagous crabs are abundant, snail shells are thicker, more sculptured, or have narrower apertures (KITCHING *et al.*, 1966; HUGHES & ELLNER, 1979; REIMCHEN, 1982), traits identified as adaptations primarily against predation (VERMEIJ, 1978). The major evidence supporting a causal relationship between predator abundance and the presence of armor is that armored shells are more resistant to crushing forces (KITCHING *et al.*, 1966; KITCHING & LOCKWOOD, 1974; CURREY & HUGHES, 1982).

Alia carinata (Hinds, 1844) (= *Mitrella carinata*) is a small (<11 mm) columbellid gastropod found abundantly in the low intertidal zone of northern California (see MORRIS *et al.*, 1980). *Alia* is especially common on the seagrasses *Phyllospadix scouleri* (Hooker) and *P. torreyi* (Watson) on open rocky shores, while it is found on *Zostera marina* (L.) on soft substrates. Preliminary observations indicated that some specimens were noticeably more keeled at the shoulder of the body whorl and that the outer apertural

lip was more crenulated (Figure 1). In this paper, we document morphological divergence in *A. carinata* and present evidence suggesting the divergence is a result of differences in predation intensity between populations.

MATERIALS AND METHODS

Our study sites were a sheltered, soft bottom harbor in Bodega Bay, California, and a rocky cove (Horseshoe Cove) just outside of Bodega Bay. *Alia carinata* were collected at both sites by combing plants by hand from base to tip in May, 1982. Shell length from base to apex and greatest width perpendicular to the axis of coiling were measured to the nearest 0.1 mm with vernier calipers. To quantify extent of keeling, a standard set of morphotypes was assembled which typified the range of keeling observed in natural populations. Five individuals were selected, ranked by extent of keeling, and assigned keel values of 1 (least keeled) to 5 (most keeled) (Figure 1). Snails sampled from the harbor and the cove were assigned keel ratings corresponding to the morphotype they most closely resembled.

To quantify the frequency of shell scars, 475 harbor snails and 343 cove snails, collected in July, 1982, were examined with a binocular dissecting microscope under low magnification. Any obscuring epibionts were gently removed with a scalpel. Chipped outer lips, broken spires, and jagged blemishes extensive enough to interrupt normal growth lines were considered predator-induced scars. Eroded shell surfaces were not considered to be scars.



Figure 1

Dorsal (above) and apertural (below) views of *Alia carinata* showing extent of keeling. Keel ratings range from 1 (far left) to 5 (far right). Shell lengths of morphotypes vary from 7.4 to 8.1 mm.

RESULTS

Harbor *Alia carinata* had a significantly greater width-to-length ratio (harbor: 0.526; cove: 0.469; $F_{(1, 306)} = 224.10$, $P < 0.01$); however, harbor and cove samples were not

significantly different in shell length. Although keeled morphotypes were present in both populations, keel ratings were significantly greater for harbor *Alia* and highly keeled forms were absent from the cove habitat (Table 1).

Table 1

Extent of keeling of *Alia carinata* collected from rocky cove and soft-bottom harbor habitats. Distribution of keel ratings differ significantly between the two study sites (Kolmogorov-Smirnov Two Sample Test: $D_{MAX} = 0.7198$; $P \ll 0.01$).

Keel rating	Cove <i>Alia</i>		Harbor <i>Alia</i>	
	Number	Percent	Number	Percent
1	117	67.24	13	9.70
2	42	24.14	13	9.70
3	15	8.62	48	35.82
4	0	0	42	31.35
5	0	0	18	13.43
Totals	174	100.00	134	100.00

The frequency of shell scars was significantly greater in the harbor. Of 475 harbor *Alia*, 164 (35.6%) had scars. Of 343 cove *Alia*, 51 (14.8%) were scarred (adjusted chi-square = 23.16, $P < 0.001$).

DISCUSSION

Our results document shell-morphology divergence between Bodega harbor and rocky shore populations of *Alia carinata*, and shell-scar data suggest that higher predation rates in the harbor may account for this divergence. Although we did not directly observe acts of predation on *Alia*, shell scars are records of past predation attempts, and shell-repair frequency is an indicator of predation intensity on a population (see VERMEIJ, 1982; VERMEIJ *et al.*, 1981). Correlation of morphological patterns and predation intensity is not sufficient evidence for the hypothesis that local selection by predators has resulted in interpopulation polymorphism. It must be shown that variation in predator-induced mortality actually exists (*i.e.*, a selective agent is acting), that present morphologies do in fact confer resistance to predation, and that local morphology has high heritability. Alternate explanations in the absence of this information include ecophenotypic effects and differential mortality among uniformly and widely dispersing larvae.

Our shell-scar data indicate that predation is a greater hazard to harbor snails than those from the cove. Thus, selection for defensive shell characteristics should be stronger in the harbor. Because *Alia carinata* lays egg capsules and has crawl-away larvae (D. Carlton, personal communication), immigration from populations lacking such selective pressure is unlikely. As a result, opportunity for divergence is enhanced (CURREY & HUGHES, 1982).

Evidence that keeled snails are more resistant to crushing is lacking. However, we have preliminary observa-

tions of prey selection by small *Cancer antennarius* (Stimpson), a predatory crab sympatric with both harbor and cove *Alia*. In 12 2-h feeding trials in which six keeled and six unkeeled snails were offered to starved *C. antennarius*, 30 unkeeled snails and 15 keeled snails were killed and consumed. In addition, 14 unkeeled snails were damaged, compared to only one keeled snail. These data are inconclusive, but suggest that keeled snails are less susceptible to crushing predation. The evidence that morphological divergence in *Alia* is related to predation is strong; however, ecophenotypic effects due to habitat differences such as water temperature and velocity, time of aerial exposure, and food availability cannot be ruled out.

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